

A TAXONOMIC REVISION OF CRAIBIODENDRON (ERICACEAE)^{1,2}

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The genus *Craibiodendron* W. W. Smith (including *Nuihonia* Dop) contains five species and is limited to southeastern Asia. It is closely related to several genera in the Andromedeae (Ericaceae) such as *Lyonia* Nutt., *Agarista* D. Don, and *Pieris* D. Don (Stevens, 1970; Judd, 1979). The group has not been revised prior to the present work. In this paper I have therefore reevaluated the limits of the genus and revised the species; nearly 300 herbarium specimens have been examined. I have attempted to employ consistent specific delimitations, compare the taxa, interpret their phylogenetic relationships, and develop descriptions and practical keys for identification.

GENERIC RELATIONSHIPS

The small genus *Craibiodendron* (Ericaceae subfam. Vaccinioideae tribe Andromedeae) was first described by W. W. Smith (1911), who then suggested that it was related to *Lyonia* and *Pieris*. In the major paper dealing with the genus prior to the present work, Smith (1912) altered his opinion and considered *Craibiodendron* to be more closely related to *Leucothoë* D. Don on the basis of its imbricate, almost free sepals, muticous anthers, and winged seeds. In 1961 Lems (note on *Henry 13137*, NY) suggested, possibly on the basis of inflorescence structure, that *Craibiodendron* is "near-ancestral" to *Pieris*. Dop (1930) segregated the very similar genus *Nuihonia* on the basis of its supposedly arillate seeds. The relationships of *Nuihonia* and other genera of Andromedeae to *Craibiodendron* are discussed briefly below.

Generic relationships within the Andromedeae have been studied by Stevens (1970, 1971) and Judd (1979), and the genera *Craibiodendron*, *Lyonia*, *Agarista*, *Pieris*, and *Leucothoë* are compared in TABLE 1. *Craibiodendron* is phenetically distinctive within the Andromedeae and is characterized by its often *superposed buds*⁴ with two (to four) bud scales and a rather elongated attachment to the twig; twigs with a homogeneous pith; petiole and leaf midrib with bifacial vascular bundles; indumentum of biseriate-stalked, small-headed, multicel-

¹The fourth in a series of revisionary studies of genera of the Andromedeae (Ericaceae). Previously studied genera include *Lyonia* (Judd, 1981), *Pieris* (Judd, 1982), and *Agarista* (Judd, 1984).

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⁴Characters in italics are unique within the *Lyonia* group of the Andromedeae.

lular hairs; axillary *panicle- to racemelike cymose inflorescences with terminal flowers* that “overwinter” within the bud; clearly imbricate calyx lobes; *often campanulate* and *carnose corollas*; papillose and geniculate filaments lacking spurs or awns; and *large, thick-walled capsules bearing a few large seeds, each with a prominent unilateral wing* (see also Judd, 1979). The species of *Craibiodendron* are also distinctive in having spherical to polygonal parenchymatous cells at the vein endings in the leaves (T. A. Rao, pers. comm.; Rao & Chakraborti, 1982). The genus is phenetically closest to *Agarista* (including *Agauria* (DC.) J. D. Hooker) and *Leucothoë* but shows differences from these genera that are of “generic magnitude” (Judd, 1979, fig. 1, table 2). *Nuihonia* (*N. sclerantha* Dop) consistently differs from *C. kwangtungense* S. Y. Hu only in having abaxially unicellular-pubescent calyx lobes; its seeds are not arillate. The genus *Nuihonia* is therefore not recognized.

Cladistically, *Craibiodendron* is most closely related to *Lyonia*. They are linked by the following synapomorphies (i.e., shared derived characters): biseriate-stalked gland-headed hairs, bifacial midrib bundles, and buds with usually two scales (the last feature, however, has undergone a reversal in *Lyonia* sect. *Maria*). *Craibiodendron* shows the autapomorphic character states of large, unilaterally winged seeds, robust capsules, and superposed buds, while the four sections of *Lyonia* are linked by the derived character states of glandular hairs with large swollen heads, bracteoles basal or nearly so, staminal spurs with disintegration tissue, and capsules with thickened sutures that often separate from the valves during dehiscence (see Judd, 1979). The presumed monophyletic group consisting of *Lyonia* and *Craibiodendron* is in turn linked with *Agarista* by the presence of geniculate filaments, and all of these are eventually linked with *Pieris* in having bands of fibers in the phloem, filament spurs (presumably lost in *Craibiodendron*, *Agarista*, and some species of *Lyonia*), and elongate testa cells (lost in some species of *Pieris*). This group of four genera also has anomocytic stomata, awnless stamens, and a chromosome number of $x = 12$; it shows a strong tendency for epidermal lignification (Judd, 1979). Stevens (1970) and Judd (1979) refer to these genera as the “*Lyonia* group.” In contrast, *Leucothoë* is cladistically isolated from these genera due to its paracytic stomata, often awned stamens, and chromosome number of $x = 11$ (Judd, 1979). *Leucothoë* is probably closer to *Zenobia* D. Don, *Gaultheria* L., *Pernettya* Gaudich., and relatives—the “*Gaultheria* group” of Stevens (1970) and Judd (1979).

It is evident from TABLE 1 and from the investigations of Stevens (1970) and Judd (1979, both phenetic and cladistic analyses) that *Craibiodendron* is more closely related to *Lyonia* and associated genera than it is to *Leucothoë*, thus supporting W. W. Smith’s (1911) suggested affinities. When the characters used by Smith (1912) to indicate relationship with *Leucothoë* are analyzed, this conclusion becomes even clearer. The imbricate calyx lobes shared by *Leucothoë* and *Craibiodendron* are a symplesiomorphy and are thus not indicative of cladistic relationship. The unilaterally winged seeds of *Craibiodendron* are not comparable to those of some species of *Leucothoë* in which the wing is formed from numerous individual cells with fringed outer walls. The winged seeds of these two genera have evolved independently and do not

TABLE 1. Variation in selected morphological and anatomical characters in *Craibiodendron* and related genera.

CHARACTER	TAXON				
	<i>Craibio- dendron</i>	<i>Lyonia</i>	<i>Agarista</i>	<i>Pieris</i>	<i>Leu- cothoë</i>
Phloem with bands of fibers	+	+	+	+	—
Glandular hairs biseriate stalked	+	+	—	+	—
Leaves					
Margin entire	+	+/-	+ (-)	+/-	—
Midrib bundle bifacial	+	+ (-)	—	- (+)	—
Stomata anomocytic	+	+	+	+	—
Epidermis lignified	+	+/-	+	+/-	—
Inflorescences "overwintering" in bud	+	+	+	—	—
Calyx lobes imbricate	+	+/-	+	—	+
Stamens					
Filaments lacking spurs	+	+/-	+	—	+
Filaments geniculate	+	+	+	- (+)	—
Anthers lacking awns	+	+	+	+	- (+)
Seeds					
Winged	+	—	—	- (+, 2 slight wings)	-/+ (bulging cells)
	(unilateral)				
Testa cells elongate	+	+	+	+/-	—

indicate close phylogenetic relationship. Finally, the stamens of *Craibiodendron* and *Leucothoë*, although similar in lacking spurs, are very different. Those of *Craibiodendron* lack appendages and have slender, geniculate filaments, while those of *Leucothoë* have awns and stout, more or less straight filaments. The morphology of the stamens indicates a closer relationship of *Craibiodendron* to *Lyonia* or *Agarista* than to *Leucothoë*.

CLADISTIC ANALYSIS

The phylogenetic relationships of the species of *Craibiodendron* were investigated using two methods: the manual Wagner Groundplan Divergence Method (Wagner, 1962, 1980); and the computer programs WAGNER, MIX (using Wagner Network Parsimony Method; described in Kluge & Farris, 1969), and PENNY (using "branch and bound" algorithm; see Hendy & Penny, 1982), which were developed by J. Felsenstein and are part of his PHYLIP package (Felsenstein, 1984). Twelve characters were used and assigned primitive (plesiomorphic) and advanced (apomorphic) states (see TABLE 2). For all characters except one a taxon was scored 0 if primitive and 1 if advanced. For character G, length of corolla lobes in comparison to length of tube, which is composed of a three-state transformation series (see TABLE 3), the most advanced state was assigned a value of 2 in the Wagner Groundplan Divergence Method; in

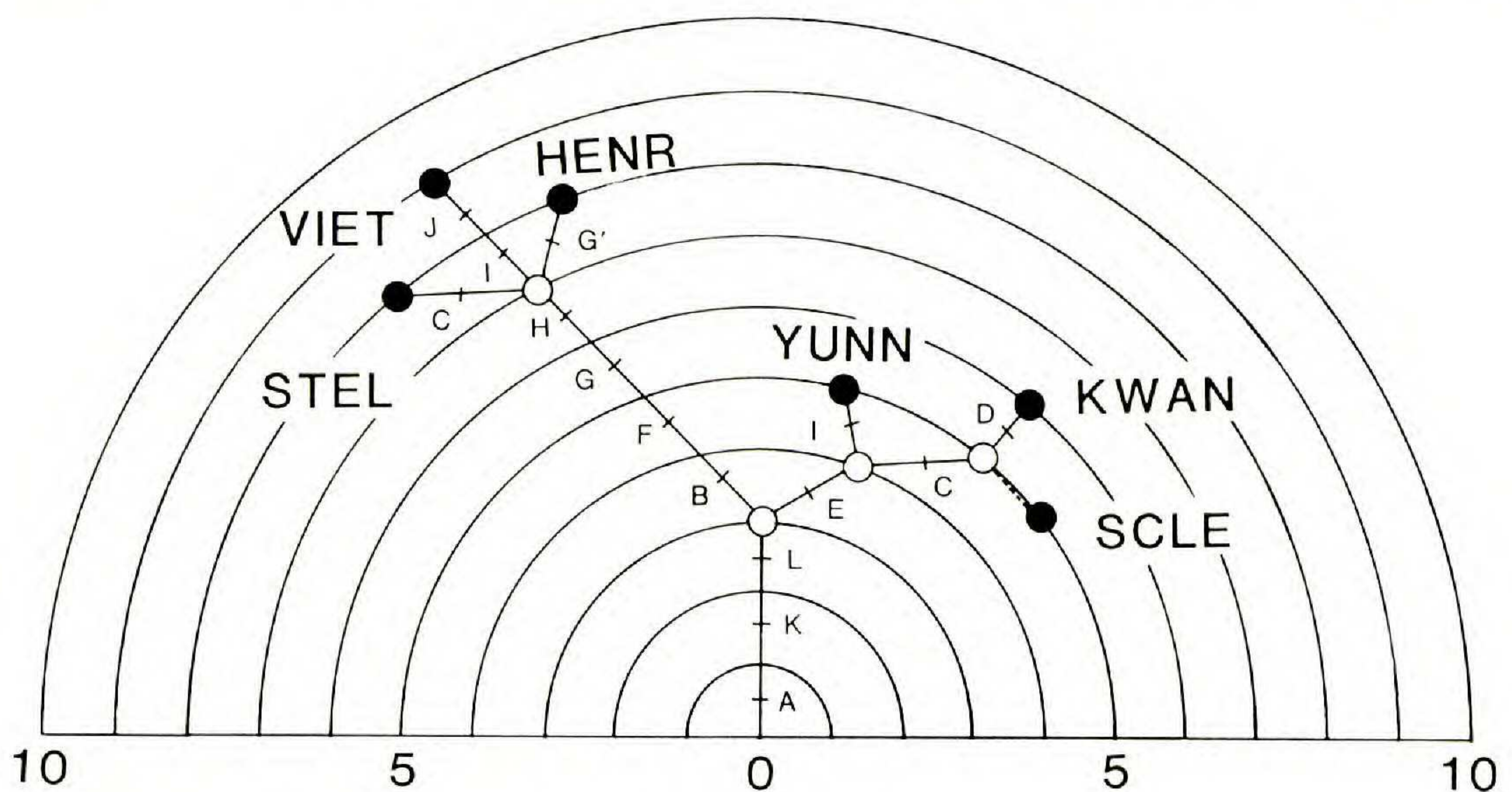


FIGURE 1. Wagner Tree for species of *Craibiodendron*: extant taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally on tree (open circles). Synapomorphies indicated on cladogram; taxon names abbreviated by first four letters of specific or varietal epithet.

the WAGNER, MIX, and PENNY computer programs the two advanced states of this character were both assigned a value of 1. TABLE 3 shows all taxa and their character-state values. For each taxon the total divergence index was determined by adding the individual character-state values. In the Wagner Groundplan Divergence Method an attempt was made to construct the shortest tree by hand, minimizing the number of both character-state reversals and parallelisms. The taxa were then plotted graphically (FIGURE 1), with the branching points determined by the mutual groupings of advanced characters and the distance by the divergence of each taxon. The computerized WAGNER, MIX, and PENNY programs also minimize the total number of character-state changes in the construction of the tree. The computer-generated trees were rooted by using a hypothetical ancestor with all plesiomorphic characters (in WAGNER) or by specifying the ancestral character states (in MIX and PENNY).

Cladistic methods require numerous assumptions concerning which is the apomorphic and which the plesiomorphic state of each character. The problems and sources of error associated with the determination of character polarity have been discussed by Stevens (1980, 1981), Crisci and Stuessy (1980), Wheeler (1981), Wiley (1981), Watrous and Wheeler (1981), Donoghue and Cantino (1984), and Maddison, Donoghue, and Maddison (1984). The consensus is that out-group analysis is the most powerful method for determining polarity; the derived states of all characters except D and E (TABLE 2) were determined by out-group comparisons (using the genera *Lyonia*, *Agarista*, and *Pieris*, successively, as out-groups; see Judd, 1979). For characters D and E, complex cymose (= monotelic) inflorescences were considered to be primitive in comparison with racemose (= polytelic) ones, following the analysis of Weberling (1965). This polarity decision results in a hypothesized loss of terminal flowers

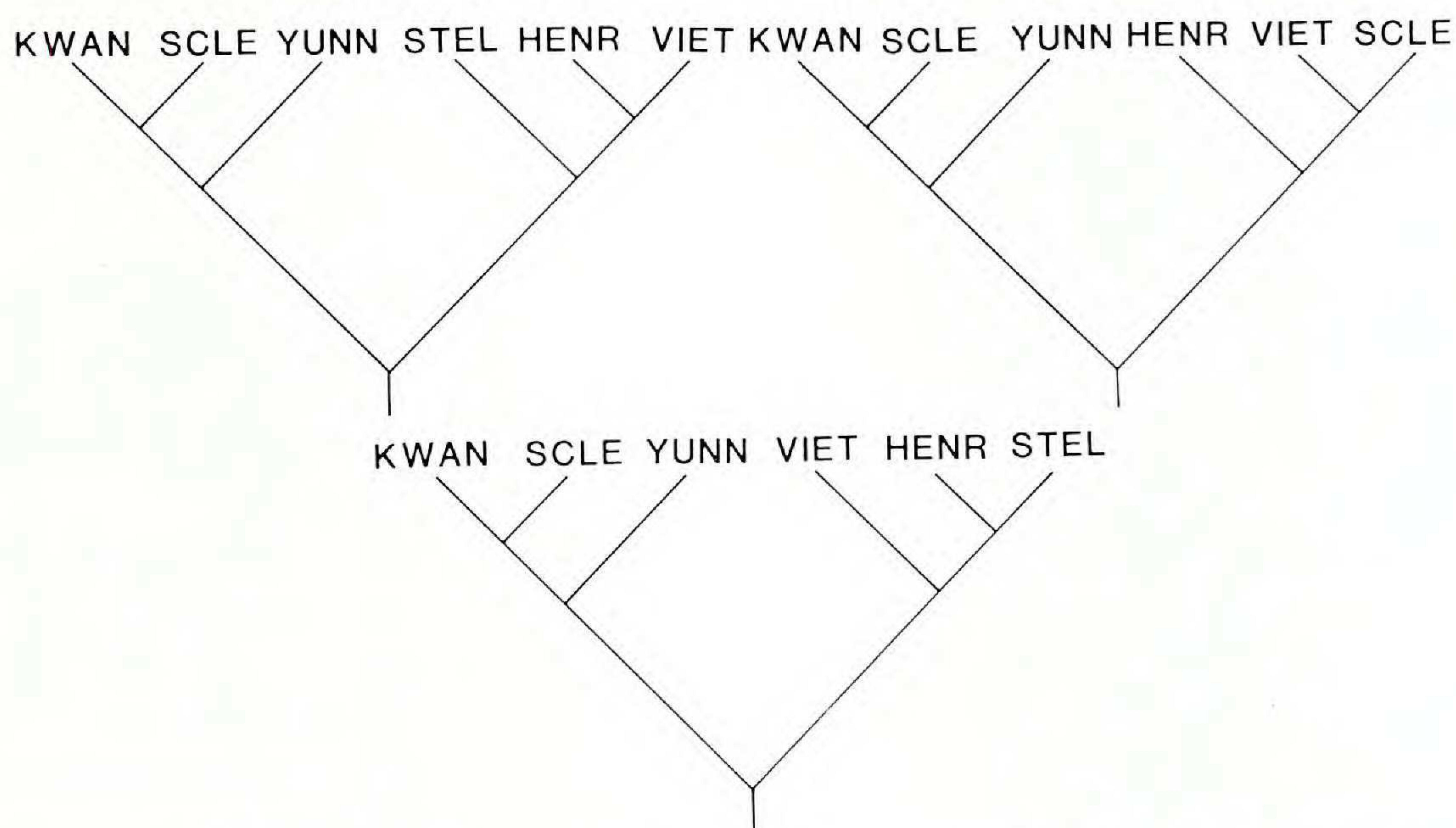


FIGURE 2. Wagner trees generated by PHYLIP programs; all require 15 steps. Taxon names abbreviated by first four letters of specific or varietal epithet.

(and the evolution of racemes) independently within *Agarista*, *Lyonia*, and *Pieris*. This may indeed have occurred, since a few species of *Agarista* (e.g., *A. pulchella* Cham. ex G. Don and *A. populifolia* (Lam.) Judd) develop inflorescences with some terminal flowers (i.e., partly monotelic), and the detailed studies of Troll (1964) have shown that cymose inflorescences are generally primitive within the Angiospermae. It is noteworthy that Lems (note on *Henry 13137*, NY, 1961) also considered the inflorescence structure (as well as the leaf venation) of *Craibiodendron* to be very primitive in the Andromedeae. However, out-group analysis leads to a reversed polarity decision for these characters; thus groupings based upon them may be suspect. The variation in inflorescence structure within the “*Lyonia* group” of the Andromedeae is indicated in FIGURE 3.

The Wagner trees (or cladograms) resulting from the above procedures (FIGURES 1, 2) indicate that the species of *Craibiodendron* may belong to two phyletic groups: the *C. scleranthum* group (including *C. scleranthum* and *C. yunnanense*) and the *C. stellatum* group (including *C. stellatum*, *C. vietnamense*, and *C. henryi*). The *C. scleranthum* group is characterized by reduced inflorescences with the secondary axes bearing from one to only ca. six flowers (E). These two species also have glabrous, urceolate to cylindrical corollas with small lobes, and stamens with long (i.e., 2.5–4 mm) filaments. This group might be paraphyletic (if polarity of character E were reversed). Members of the *C. stellatum* group are characterized by campanulate corollas (F) with large lobes (G) that are often unicellular-pubescent (H). The leaves of this group often show impressed secondary and/or tertiary veins (B). The filaments of these species are typically shorter (i.e., 1.5–2.7 mm) than those of the *C. scleranthum* group.

Both groups share the derived character states of often-superposed buds (A),

robust capsules (K), and large, unilaterally winged seeds (L). They are very similar in vegetative and fruit characters, being best distinguished by floral features (see key). *Craibiodendron yunnanense* and *C. scleranthum* are likely the most phenetically primitive extant members of the genus.

The trees resulting from the Wagner Groundplan Divergence Method and Felsenstein's WAGNER, MIX, and PENNY computer programs scarcely differ, which is not unexpected in this small and relatively simple data set; all shortest trees are the same length (15 steps). The only differences are in the resolution of the trichotomy (in the Wagner Groundplan Divergence tree) involving taxa of the *Craibiodendron stellatum* group (see FIGURES 1 and 2). These minor differences probably result from the fact that the procedure that prints out the trees and the internal data structures used in the PHYLIP package of computer programs cannot handle trichotomies. Therefore, trichotomies are expressed as a series of dichotomies, with some branches of zero length (see PHYLIP documentation—Felsenstein, 1984).

DISTRIBUTION

All five species of *Craibiodendron* are limited to southeastern Asia (southern China, eastern India, Burma, Laos, Thailand, Cambodia, and Vietnam), and the group is basically montane, extending from ca. 200 to 3200 m altitude. The center of diversity is in southeastern Yunnan (China), where three species occur. *Craibiodendron stellatum* is the most widely distributed species (see MAP 3), while *C. vietnamense* and *C. scleranthum* var. *scleranthum* are both endemic to very small areas in southern Vietnam (see MAPS 1, 2). The species of *Craibiodendron* tend to be allopatric or only marginally sympatric.

It is of interest that several taxa show strange disjunct distribution patterns. *Craibiodendron stellatum* occurs commonly from southern Yunnan and adjacent Burma to northern Thailand and has scattered disjunct populations southward, extending to the Bi-Doup region of southern Vietnam (MAP 3). A similar disjunction is seen between the northern *C. henryi* and its close relative *C. vietnamense*, the latter also limited to the Bi-Doup region. Finally, in the *C. scleranthum* group, *C. scleranthum* var. *kwangtungense* and *C. yunnanense* are distributed in southern China and adjacent Burma, while *C. scleranthum* var. *scleranthum* has only been collected in southern Vietnam (near Nha-trang). A similar north-south disjunction pattern is seen in *Lyonia*, where *L. ovalifolia* (Wallich) Drude var. *rubrovenia* (Merr.) Judd occurs in both Hainan and southern Vietnam (Judd, 1981). These southern disjunct localities may represent relict populations—indicating a southward displacement of species ranges (during the Pleistocene) relative to their present positions.

TAXONOMIC CRITERIA

Entities that have no major internal morphological discontinuities and show separation from other similar entities by consistent morphological gaps are considered to be species. Species of *Craibiodendron* frequently are distinguished by floral morphology, inflorescence structure, and leaf shape and apex. Such entities have definite geographic distributions and ecological preferences. All

TABLE 2. Characters used in the cladistic analyses of the species and varieties of *Craibiodendron*.

CODE	CHARACTER	PRIMITIVE STATE	ADVANCED STATE
A	Buds	1 per node	Often superposed, 2 or 3 per node
B	Adaxial leaf venation	2° veins not impressed	2° and/or 3° veins at least sometimes impressed
C	Leaf apex	Acuminate or long-acuminate	Acute to rounded or retuse
D	Inflorescence structure	2° and sometimes 3° axes present (panicle-like)	Only 1° axes present (racemelike)
E	2° inflorescence axes	With 7 to 30 flowers	With 1 to 6 flowers
F	Corolla shape	Urceolate or cylindrical	Campanulate
G	Corolla lobes	Small (much less than ½ length of tube)	1: large (ca. ½ length of tube) 2: very conspicuous (much longer than tube)
H	Corolla pubescence	Glabrous	At least sometimes sparsely to moderately pubescent
I	Corolla epidermal cells	± smooth to slightly bulging	Usually papillose
J	Style	Glabrous	Unicellular-pubescent
K	Capsule	Small to moderate-sized	Robust
L	Seeds	Not winged	Unilaterally winged

are rather widespread (see MAPS 1–3) except for *C. vietnamense*, which is limited to a small area of southern Vietnam. Most species appear to be only marginally sympatric. *Craibiodendron stellatum* and *C. vietnamense*, however, both occur in the Bi-Doup area of Vietnam, and there is some distributional overlap in southern Yunnan. The marginally sympatric *C. stellatum* and *C. henryi* differ somewhat in elevational range, with the former occurring from ca. 200 to 1950 m and the latter from 1500 to 2850 m altitude. There may be occasional hybridization when species occur together—for example, in southern Yunnan between *C. stellatum* and *C. henryi* (see discussion under *C. henryi*).

The taxonomic usefulness of (and the variation within) the characters differing within the genus are discussed below. Characters most useful in species delimitation include corolla shape, size, color, and indumentum; leaf shape and apex type; inflorescence structure (number of branch orders, size, number of flowers per secondary axis); capsule and seed size; calyx size and indumentum; and filament length.

HABIT

The habit of species of *Craibiodendron* is quite variable. Depending upon habitat, plants of each species can grow as small shrubs or moderate-sized (to 10–20 m tall) trees. The bark is consistently gray and longitudinally furrowed.

As in the other members of the Andromedeae (see Lems, 1962; Judd, 1981, 1982, 1984), the shoot meristem in *Craibiodendron* has a limited life span, and growth in height is achieved by a succession of equivalent, axillary, orthotropic shoots. All species show a slight variation of Leeuwenberg's model of growth (see Hallé, Oldeman, & Tomlinson, 1978, for description). Floral buds are produced in the leaf axils of the distal portion of the shoots, and the shoot apex aborts. The inflorescences overwinter within the buds, with meiosis presumably occurring in the spring.

The branches vary from terete to slightly angled, and the pith is homogeneous (Stevens, 1971).

INDUMENTUM

The indumentum of *Craibiodendron* is of three distinct types: unicellular hairs; multicellular, biseriate-stalked hairs with small glandular heads; and papillae. The distribution of glandular hairs is too uniform to be of taxonomic value within the genus. However, the distribution and density of unicellular hairs are often taxonomically significant. For example, the pubescence of the abaxial surface of the calyx lobes allows the differentiation of two geographically isolated varieties of *C. scleranthum*, while the presence of unicellular hairs on the style of *C. vietnamense* assists in separating it from *C. henryi*. The corollas of *C. scleranthum* and *C. yunnanense* are consistently glabrous, while those of *C. stellatum* are moderately to densely pubescent. It is of interest that both glabrous and pubescent corolla forms of *C. henryi* occur throughout the range of this species.

The distribution of papillae is rather uniform in the genus. They occur on the filaments of all species, and they (or at least slightly bullate cells) are frequent on the corolla, especially on the overlapping portions of the lobes. The corollas of *Craibiodendron yunnanense* are usually conspicuously papillose, thus aiding in separating this species from *C. scleranthum*, a taxon with smooth to only obscurely papillose corollas.

LEAVES

Although leaf blades tend to be quite variable in size even within a single species (e.g., 4.3–15.5 cm long in *Craibiodendron yunnanense*, 3–17 cm long in *C. stellatum*), this character is slightly useful in separating *C. scleranthum* var. *scleranthum* from var. *kwangtungense*. Lamina shape varies from ovate to obovate and typically shows much infraspecific variation. However, lamina shape is helpful in distinguishing between the varieties of *C. scleranthum* (see key), and between sterile specimens of *C. henryi* and *C. yunnanense*. The leaf apex varies from retuse or rounded to long-acuminate and is an important taxonomic character (see key); it provides a valuable means of distinguishing *C. scleranthum* from *C. yunnanense*, and *C. stellatum* from both *C. vietnamense* and *C. henryi*.

Although there are no major differences in venation pattern within the group, the secondary and tertiary veins are slightly to clearly impressed in some leaves

TABLE 3. Character divergence values for taxa used in cladistic analyses.

TAXON*	CHARACTER												Total
	A	B	C	D	E	F	G	H	I	J	K	L	
<i>stellatum</i>	1	1	1	0	0	1	1	1	0	0	1	1	8
<i>henryi</i>	1	1	0	0	0	1	2	1	0	0	1	1	8
<i>vietnamense</i>	1	1	0	0	0	1	1	1	1	1	1	1	9
<i>yunnanense</i>	1	0	0	0	1	0	0	0	1	0	1	1	5
<i>scleranthum</i>	1	0	1	0	1	0	0	0	0	0	1	1	5
<i>kwangtungense</i>	1	0	1	1	1	0	0	0	0	0	1	1	6

* Each taxon is indicated by its specific or varietal epithet.

but flat or slightly raised in others. This variation often provides a useful means of distinguishing between sterile specimens of *Craibiodendron henryi* and *C. yunnanense*.

Craibiodendron has lignified epidermal cells and transcurrent secondary veins (Stevens, 1971). Stevens (1969, 1971) also reported that the leaves of some plants show the development of a hypodermis and/or lignified spongy mesophyll, or fibers in the mesophyll.

INFLORESCENCES

The flowers of *Craibiodendron* are borne in distinctive axillary raceme- to paniclelike cymes on branches of the previous season. There may be one or two (rarely three) inflorescences per leaf axil. Terminal flowers are always present on the inflorescence axes, so the inflorescences are monotelic (= cymose or determinate—see Weberling, 1965). This inflorescence type is, according to Weberling (1965), more primitive than the polytelic type (= racemose or indeterminate), in which no terminal flowers are formed and the apices merely abort. Monotelic inflorescences are uncommon in the Ericaceae, occurring elsewhere only in *Elliottia* Muhlenb. ex Ell. (Bohm *et al.*, 1978) and a few species of *Agarista* (Judd, 1984). The size and structure of the cymose inflorescences of *Craibiodendron* are valuable taxonomic characters (see key). The inflorescences may be large and many-flowered with two or three branch orders (i.e., development of first- and second-order paracladia) or reduced to few-flowered racemelike structures with only one branch order (i.e., only main axis present) (see FIGURE 3). There is considerable variation in structure from the solitary lateral bibracteolate flowers (of the racemelike cymes of *C. scleranthum* var. *kwangtungense*) through short secondary branches bearing usually three to six flowers, each (except terminal flower) subtended by a small bract and with two bracteoles (in the narrow paniculate cymes of *C. yunnanense*) to elongate and branched secondary axes bearing usually seven to 30 flowers (in the broad, lax, paniclelike cymes of *C. henryi* or *C. stellatum*)—see FIGURES 3–8. The inflorescences also vary in length, from only 1–8 cm in *C. scleranthum* to 6–30 cm in *C. henryi*.

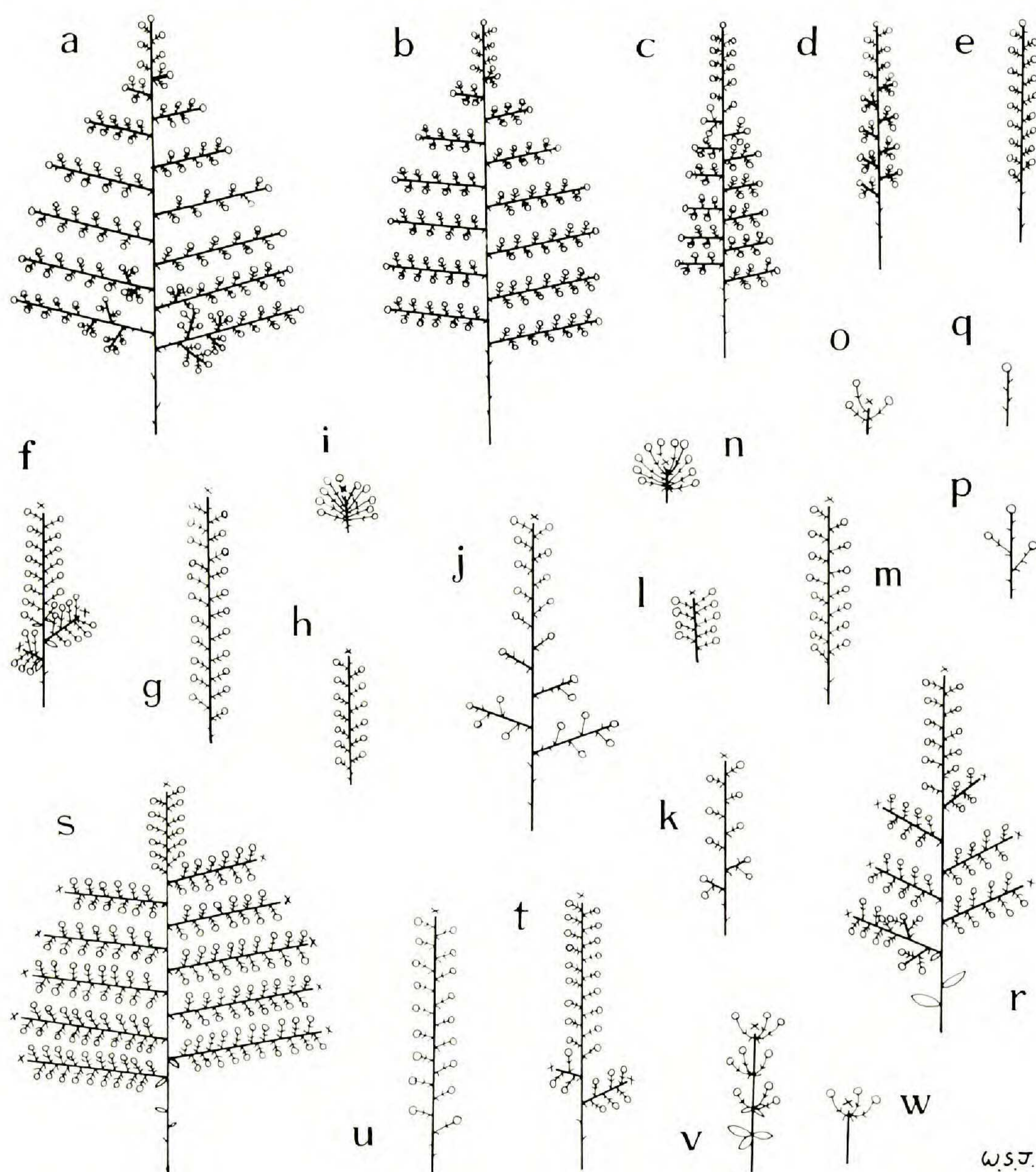


FIGURE 3. Inflorescence form in "Lyonia Group" of Andromedeae: a-e, *Craibiodendron*, axillary panicle- to racemelike cymes; f-i, *Lyonia*, axillary panicles, racemes, fascicles; j-r, *Agarista*, axillary or less commonly terminal panicles (sometimes partly cymose), racemes, fascicles, few-flowered clusters (with or without terminal flowers), solitary flowers; s-w, *Pieris*, axillary or terminal panicles, racemes (some with whorled flowers). Flowers indicated by circles; aborted apex (= lacking terminal flower) indicated by "x."

FLOWERS

The flowers of *Craibiodendron* are five- (rarely four- or six-)merous and usually fragrant.

The pedicel varies in length from 1 to 7 mm, showing extreme variability since it tends to elongate as the flowers and fruits develop. All species have a clearly developed articulation between the pedicel and the receptacle, its po-

sition varying from at to ca. 1.5 mm below the insertion of the calyx. The pedicel of a lateral flower is always subtended by a single bract and has two alternate to opposite bracteoles positioned from near its base to the midpoint. The number, size, shape, and position of the bracts and bracteoles associated with lateral flowers are too uniform to be useful at the species level. Flowers terminating inflorescence axes may have no bracteoles, or one or two (rarely three) of them. In other genera of Andromedaceae, the distinction between bracts and bracteoles does not become arbitrary as it does in *Craibiodendron*. For example, the bracteoles of lateral flowers would be considered bracts if they each subtended higher-order flowers, as often occurs, thus forming a dichasium. Bracts and bracteoles are often quickly deciduous.

The calyx lobes show some interspecific difference in size (e.g., 1–1.3 mm wide in *Craibiodendron vietnamense*, vs. 1.2–2.3 mm in *C. henryi*), but in general there is little variation in this structure.

Corolla shape is extremely useful in delimiting infrageneric taxa within the genus (see key). The corollas of *Craibiodendron yunnanense* and *C. scleranthum* are urceolate to cylindrical with small lobes, while those of *C. stellatum*, *C. vietnamense*, and *C. henryi* are campanulate and more deeply lobed (especially prominently so in *C. henryi*). It varies from white (e.g., *C. stellatum* and *C. henryi*) to often red or purple (e.g., *C. yunnanense*). Its length varies from ca. 2–3.5 mm in *C. vietnamense* and *C. henryi* to 4–6 mm in *C. yunnanense*. Corolla size aids in distinguishing *C. stellatum* from *C. henryi* and *C. vietnamense*, and in differentiating these three species from *C. yunnanense* and *C. scleranthum* (see key).

Staminal-filament length ranges from 1.5–2 mm in *Craibiodendron henryi* to 3.3–4 mm in *C. yunnanense*; it is generally greater in species with urceolate flowers. Androecial characters, except for filament length, are very consistent within *Craibiodendron* and have not been used at the species level.

Ovary shape varies from ovoid to subglobose. Gynoecial characters show little variation within the genus.

FRUITS AND SEEDS

The fruits of *Craibiodendron* are robust, thick-walled, usually five-valved, subglobose or short-ovoid, loculicidal capsules. Capsule size varies from 13–18 by 14–25 mm in *C. scleranthum* to only 6–11 by 7–13 mm in *C. yunnanense*. The distinctive seeds are large, brown, and ovoid, with a prominent unilateral wing; they have a thin testa composed of elongate cells. Seed length varies from 4–7 mm in *C. yunnanense* to 8–12.5 mm in *C. scleranthum* and is thus of some taxonomic value at the species level.

TAXONOMIC TREATMENT

Craibiodendron W. W. Smith, Rec. Bot. Surv. India **4**: 276. 1911. TYPE: *Craibiodendron shanicum* W. W. Smith (= *C. stellatum* (Pierre) W. W. Smith).

Nuihonia Dop in M. Lecomte, Fl. Gén. Indo-Chine **3**: 719. 1930. TYPE: *Nuihonia sclerantha* Dop (= *Craibiodendron scleranthum* (Dop) W. Judd).

Evergreen shrubs or trees with gray, shallowly and longitudinally furrowed bark. Indumentum of unicellular hairs, multicellular, biseriate-stalked hairs with small glandular heads, and papillae. Branches terete to slightly angled, often with sparse scattered gland-headed hairs, pith homogeneous. Buds often superposed, nearly hemispheric to broadly conical, with 2 (to 4) imbricate scales. Leaves alternate, simple, petiolate, convolute in bud, often reddish on young shoots; lamina coriaceous, with scattered (and often quickly deciduous) gland-headed hairs on both surfaces, often with unicellular hairs on adaxial surface of midvein, especially proximal portion, the margin entire, the venation brochidodromous, midvein impressed adaxially, secondary and tertiary veins slightly raised abaxially, tertiary veins reticulate, petiole vascular bundle bifacial. Inflorescences overwintering within bud, presumably with meiosis occurring after emergence, axillary from upper nodes of previous year's growth, of panicle- to racemelike cymes, often 2 per node; axes with scattered gland-headed hairs; flowers pendulous, perfect, 5- (rarely 4- or 6-)merous, usually fragrant, in axil of small bract or terminating axes, with 2 (on terminal flowers sometimes 0 or 1, very rarely 3) bracteoles near base to midpoint of pedicel; pedicel elongating as flower and fruit develop, with gland-headed hairs. Calyx of usually 5 imbricate lobes, articulate with pedicel, persistent in fruit, adaxially densely to moderately pubescent, abaxially with stomata, margin fringed with unicellular hairs; corolla urceolate or cylindrical to campanulate, with usually 5 short to long, imbricate lobes, carnose, cream or white to red or gray-purple, the outer surface glabrous to densely covered with unicellular hairs and with stomata, sometimes slightly papillose, the inner surface glabrous and lacking stomata; stamens usually 10, in 2 whorls, inserted at base of corolla, the filament slightly flattened, geniculate, obscurely to clearly papillose, somewhat expanded near base, lacking spurlike appendage, the anther more or less ovoid, minutely papillose to nearly smooth, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, with white line of disintegration tissue on back of each lobe, the pollen tricolporate, in tetrahedral tetrads, without viscin strands; stigma truncate, obscurely 5-lobed, minutely papillose, the style columnar, slightly swollen near base, straight, with 5-fluted central canal, slightly impressed into apex of ovary and usually slightly exserted, the ovary superior, usually 5-locular, glabrous to densely covered with unicellular hairs, with placentae axile, subapical on persistent columella, slightly bilobed, bearing anatropous ovules; nectariferous disc an enlargement of base of ovary wall, slightly lobed. Capsules erect, thick-walled, robust, loculicidal, subglobose to short-ovoid or ovoid, sutures unthickened and not separating from valves at dehiscence, placentae persistent on columella. Seeds large, brown, ovoid with conspicuous unilateral wing, the testa thin, composed of single layer of usually elongate, thin-walled cells; embryo small, straight, more or less allantoid, white, with 2 small cotyledons, central in cross section, surrounded by fleshy endosperm.

The name *Craibiodendron* honors William G. Craib (1882–1933), of the Royal Botanic Gardens, Kew (Smith, 1911).

DISTRIBUTION. Southeast Asia—China (Tibet, Yunnan, Guangxi, Guangdong),

eastern India (Arunachal Pradesh, Meghalaya, Nagaland), and Burma, south to Laos, Thailand, Cambodia, and Vietnam.

NUMBER OF SPECIES (TAXA). 5 (6).

MEASUREMENTS AND TERMINOLOGY

All measurements (except plant height and flower color, which were taken from information given on specimen labels) included in the descriptions of species come directly from dried herbarium material. As used here, "glabrous" and "pubescent" refer to the presence or absence of unicellular hairs; the presence and distribution of multicellular, gland-headed hairs are described separately.

SPECIMENS EXAMINED

In the citation of specimens, abbreviations of institutions follow the seventh edition of *Index Herbariorum* (Holmgren, Keuken, & Schofield, 1981). In order to conserve space, only selected specimens have been cited.

KEY TO THE SPECIES OF CRAIBIODENDRON

1. Corolla 4–6 mm long, urceolate to cylindrical, glabrous, lobes less than $\frac{1}{4}$ of total length; inflorescence a raceme- to paniclelike cyme, often quite narrow, longest secondary axes with ca. 1 to 6 (to 8) flowers.
 2. Leaf apex (retuse or) rounded to acute or short-acuminate; inflorescence a racemelike cyme to a reduced paniclelike cyme, secondary axes with at most 3 flowers; capsules 13–18 by 14–25 mm; seeds 8–12.5 mm long; corolla smooth to obscurely papillose; [Guangdong and Guangxi, China; Vietnam]. 2. *C. scleranthum*.
 2. Leaf apex long-acuminate; inflorescence a paniclelike cyme, often quite narrow, longest secondary axes with usually 3 to 6 (to 8) flowers; capsules 6–11 by 7–13 mm; seeds 4–7 mm long; corolla clearly papillose; [Yunnan and Tibet, China]. 1. *C. yunnanense*.
1. Corolla 2–4.5 mm long, campanulate, glabrous to densely pubescent, lobes at least $\frac{1}{2}$ of total length; inflorescence a paniclelike cyme, often quite broad, longest secondary branches with ca. 6 to 30 flowers.
 3. Leaves rounded to retuse or acute; corolla moderately to densely pubescent, 3–4.5 mm long; [southern Yunnan and Guangxi, China; Burma; Laos; Thailand; Cambodia; Vietnam]. 5. *C. stellatum*.
 3. Leaves usually long-acuminate or acuminate (rarely acute); corolla glabrous to moderately pubescent, 2–3.5 mm long.
 4. Corolla lobes more or less equal to tube, the surface clearly to obscurely papillose and sparsely to very sparsely pubescent; calyx lobes ca. 1–1.3 mm wide; style pubescent; [Vietnam]. 4. *C. vietnamense*.
 4. Corolla lobes usually much longer than tube, the surface glabrous to moderately pubescent, with papillae limited to overlapping, marginal areas of lobes; calyx lobes 1.2–2.3 mm wide; style glabrous; [India; Yunnan, China; northern Burma; northern Thailand]. 3. *C. henryi*.

1. ***Craibiodendron yunnanense*** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 5: 159. 1912. TYPE: China, Yunnan, vicinity of Yunnan-sen, *E. E. Maire*

1790 (lectotype, here selected, E; photo of lectotype, B!; isoelectotype, E!).

FIGURE 4.

Tree or shrub to 11 m tall. Twigs glabrous to sparsely pubescent. Buds 2 per node, sometimes superposed, with 2 (to 4) scales. Leaves with petiole 2–13 mm long; blade elliptic or oblong to obovate (or ovate), 4.3–15.5 by 1.5–3.8 cm, apex long-acuminate, base cuneate and sometimes slightly attenuate, margin plane to slightly revolute near base, secondary and tertiary veins usually slightly raised to flat adaxially, midvein glabrous to sparsely pubescent near petiole (along lower $\frac{1}{2}$). Inflorescences paniclelike cymes 4.5–20 cm long, with 2 orders of branches, longest secondary branches with 2 to 6 (to 8) flowers, axes essentially glabrous to sparsely pubescent. Pedicels 1–6 mm long, very sparsely to sparsely pubescent; bracteoles alternate to sometimes subopposite, near base to midpoint of pedicel, narrowly triangular to triangular-ovate, 0.5–1.9 mm long; bracts linear or narrowly triangular to narrowly ovate, 1.2–6.5 mm long, very quickly deciduous. Calyx lobes broadly ovate-triangular with acuminate to rounded-mucronate apices, 0.9–1.5 by 1.2–2.2 mm, abaxial surface glabrous; corolla urceolate to cylindrical, 4–6 by 1.5–4 mm, lobes very small in comparison with tube, cream to red or gray-purple, with abaxial surface glabrous but usually clearly papillose (especially in distal portion), thickened ridges not evident; stamens with filament 3.3–4 mm long, anther 0.7–1 mm long; ovary glabrous, style glabrous. Capsules subglobose or short-ovoid to ovoid, 6–11 by 7–13 mm, glabrous; seeds 4–7 mm long.

DISTRIBUTION AND ECOLOGY. China (Yunnan, Tibet) and northern Burma (MAP 1). Thickets and open rocky areas, temperate to warm-temperate forests, margins of coniferous forests; 1500–3200 m alt. Flowering (May) June through early August (October).

REPRESENTATIVE SPECIMENS. **Burma:** W flank of N'Maikha-Salwin divide, 26°17'N, 98°46'E, *Forrest* 27053 (A, E, K), 26°15'N, 98°45'E, *Forrest* 27251 (A, K, US, W). **China.** **TIBET:** Burma-Tibet frontier, 28°25'N, 97°55'E, *Kingdon-Ward* 10149 (BM). **YUNNAN:** Mingkwong Valley, 25°15'N, *Forrest* 7990 (BM, E, K); NW of Tengyueh, 25°10'N, *Forrest* 8218 (BM, E, K, S); Shweli Valley, 25°N, *Forrest* 8239 (E); Mekong and Tung-chang divide, 25°20'N, *Forrest* 12131 (E); Ghi-Shan, E of Tali Lake, 25°48'N, *Forrest* 13522 (BM, E, MO); Tali Range, *Forrest* 15592 (A, E, K), 15626 (E, K); between Sha-yang and Chutong, 25°20'N, 99°36'E, *Forrest* 21068 (A, E, K, US); Mengtze, *Henry* 9182 (A, K); Lo Shiueh Mtn., Lichiang Range, *McLaren's Coll.* U106 (A, BM, E, UC); Yao-chou, Tengyueh and Lungling, *Rock* 7131 (A, US); between Kambaiti and Tengyueh, *Rock* 7567 (A, UC, US); Shang-pa Hsien, *Tsai* 54896 (A); Che-tse-lo, *Tsai* 58394 (A, E); Ta-li Hsien, *Wang* 71728 (A); Kuikiang Valley, Tzron, Bucahwang, *Yü* 21046 (A, E).

Craibiodendron yunnanense is most closely related to the geographically isolated *C. scleranthum* (see MAP 1), from which it differs chiefly in having long-acuminate leaves, broader paniclelike cymes with longer secondary axes bearing ca. 3 to 6 (to 8) flowers, and smaller fruits and seeds. In addition, the multicellular gland-headed hairs on the abaxial leaf surface are more conspicuous in *C. yunnanense* than in *C. scleranthum*. However, sterile or fruiting specimens are often quite difficult to distinguish from the partially sympatric *C. henryi* (a species with distinctly different flowers—see key). Such material

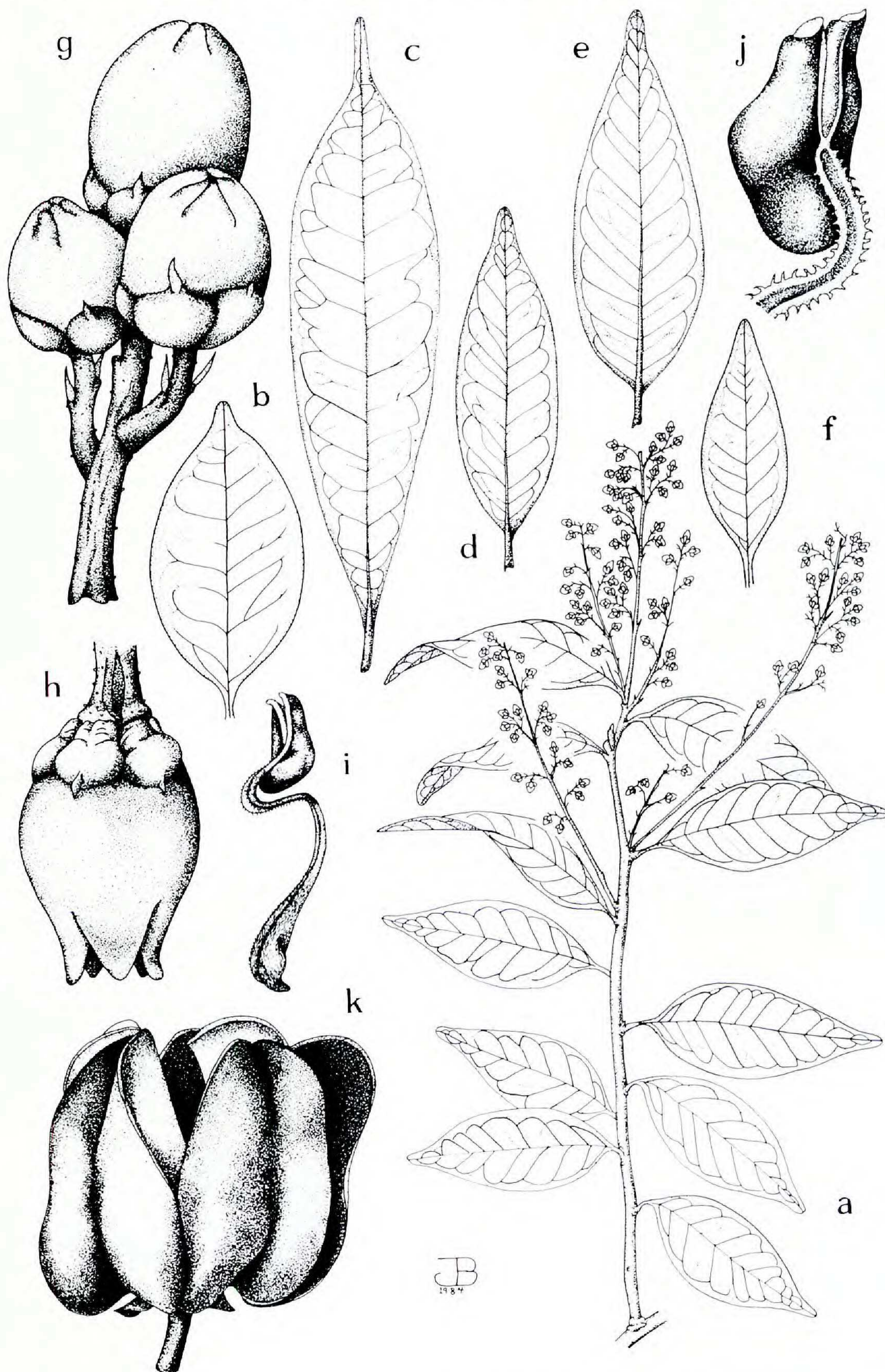
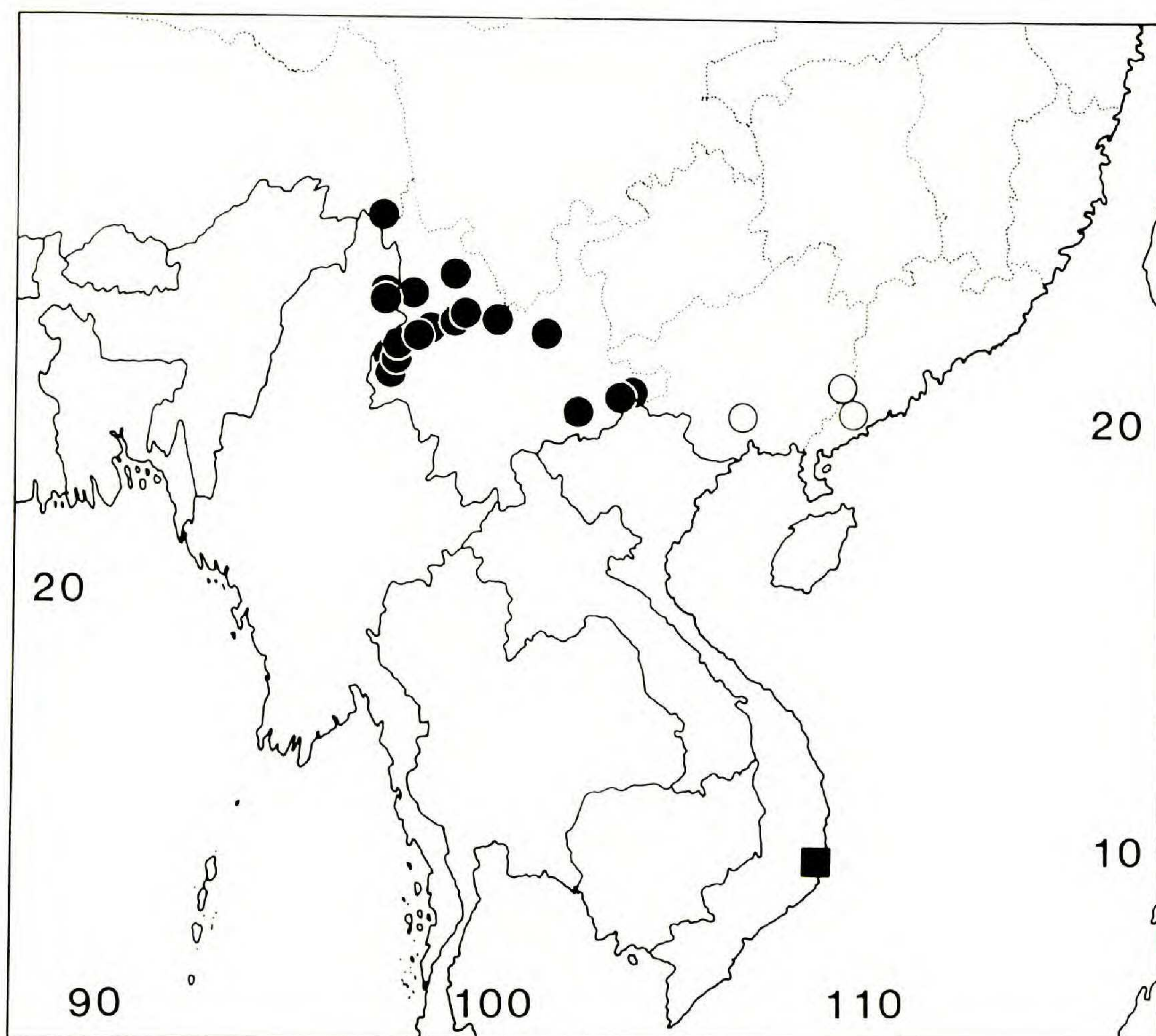


FIGURE 4. *Craibiodendron yunnanense*: a, segment of twig with inflorescences, $\times 0.3$; b–f, leaves, $\times 0.5$; g, dichasium, $\times 5$; h, flower, $\times 5$; i, stamen, $\times 10$; j, anther, $\times 25$; k, capsule, $\times 5$.



MAP 1. Distribution of *Craibiodendron yunnanense* (black circles), *C. scleranthum* var. *scleranthum* (square), and *C. scleranthum* var. *kwangtungense* (open circles).

cannot be keyed, but useful characters include the more frequently elliptic to obovate leaves of *C. yunnanense* (vs. usually elliptic to ovate in *C. henryi*), the nonimpressed (vs. often impressed) secondary and tertiary veins, and the narrower infructescences.

Earlier illustrations of this species can be found in Smith (1912) and Anonymous (1974).

2. *Craibiodendron scleranthum* (Dop) W. Judd, comb. nov.

Tree or shrub to 20 m tall. Twigs glabrous to sparsely pubescent. Buds 1 or 2 per node (superposed if 2), with 2 (to 4) scales. Leaves with petiole 4–13 mm long; blade elliptic or nearly oblong to obovate or ovate, 3.2–10 by 1.2–4.6 cm, the apex (retuse or) rounded to acute or short-acuminate, the base cuneate to attenuate, the margin plane to slightly revolute, especially near base, the secondary and tertiary veins usually slightly raised adaxially, the midvein glabrous to very sparsely pubescent near petiole (along lower $\frac{1}{2}$). Inflorescences racemelike or narrow (poorly branched) paniclelike cymes 1–8 cm long, with 1 or 2 orders of branches, longest secondary branches represented by single

(bracteolate) flower or with at most 3 flowers (dichasium), axes sparsely to densely pubescent. Pedicels 1–6 mm long, sparsely to densely pubescent; bracteoles alternate to opposite, at base to within lower $\frac{1}{3}$ (occasionally to midpoint) of pedicel, narrowly triangular to linear, 0.2–1.2 mm long; bracts narrowly triangular to narrowly ovate, 0.4–2.5 mm long, deciduous. Calyx lobes broadly ovate-triangular with acuminate to acute or obtuse apices, 1.2–2(–2.5) by 1.6–2.5 mm, abaxial surface glabrous or sparsely to moderately pubescent; corolla urceolate to cylindrical, 4–6 by 2–3.5 mm, lobes small in comparison with tube, cream to red, with abaxial surface glabrous, smooth to obscurely papillose distally, thickened ridges not evident; stamens with filament 2.5–3.6 mm long, anther 0.6–1 mm long; ovary glabrous to sparsely (rarely? moderately) pubescent, style glabrous. Capsules subglobose or globose to short-ovoid, 13–18 by 14–25 mm, glabrous to very sparsely pubescent; seeds 8–12.5 mm long.

DISTRIBUTION. China (Guangdong and Guangxi) and southern Vietnam.

Key to the Varieties of *Craibiodendron scleranthum*

- Abaxial surface of calyx glabrous; leaf blades 2.5–6.3 cm long, obovate to elliptic; [Vietnam]. 2a. var. *scleranthum*.
 Abaxial surface of calyx sparsely to densely pubescent (i.e., with unicellular hairs); leaf blades (3.6–)4–9.6 cm long, ovate to elliptic or occasionally slightly obovate; [Guangdong and Guangxi]. 2b. var. *kwangtungense*.

2a. *Craibiodendron scleranthum* (Dop) W. Judd var. *scleranthum*

FIGURE 5a–c.

Nuihonia sclerantha Dop in M. Lecomte, Fl. Gén. Indo-Chine 3: 719. 1930. TYPE: Vietnam, Nui-hon-heo, near Nha-trang, 3 May 1923, E. Poilane 6236 (holotype, P; isotypes, A!, B!, K!, L(fragment)!).

Tree to 12 m tall. Leaf blades obovate to elliptic, 2.5–6.3 by 1.1–2.8 cm. Inflorescences narrow (poorly branched) panicle- to racemelike cymes, secondary branches supporting 1 to 3 flowers. Abaxial surface of calyx lobes glabrous. Capsules not seen.

See Dop (1930) for an earlier illustration of this variety.

DISTRIBUTION AND ECOLOGY. Vietnam, montane region near Nha-trang (MAP 1). Flowering in May.

REPRESENTATIVE SPECIMENS. Known only from type collection.

2b. *Craibiodendron scleranthum* (Dop) W. Judd var. *kwangtungense* (S. Y. Hu) W. Judd, comb. et stat. nov.

FIGURE 5d–l.

Craibiodendron kwangtungense S. Y. Hu, J. Arnold Arbor. 35: 198. 1954. TYPE: China, Kwangtung [Guangdong], Ting-Wu-Shan, West River, 5 July 1928, Y. Tsiang 792 (lectotype, here selected, A!; isoelectotypes, K!, NY!, UC!, W!).

Craibiodendron kwangtungense S. Y. Hu var. *frutescens* S. Y. Hu, J. Arnold Arbor. 35: 199. 1954. TYPE: China, Kwangsi [Guangxi], SE of Shang-sze, Shap-man-tai-shan, near Iu Shan village, 10 May 1933, W. T. Tsang 22252 (holotype, A!; isotypes, BM!, S!).

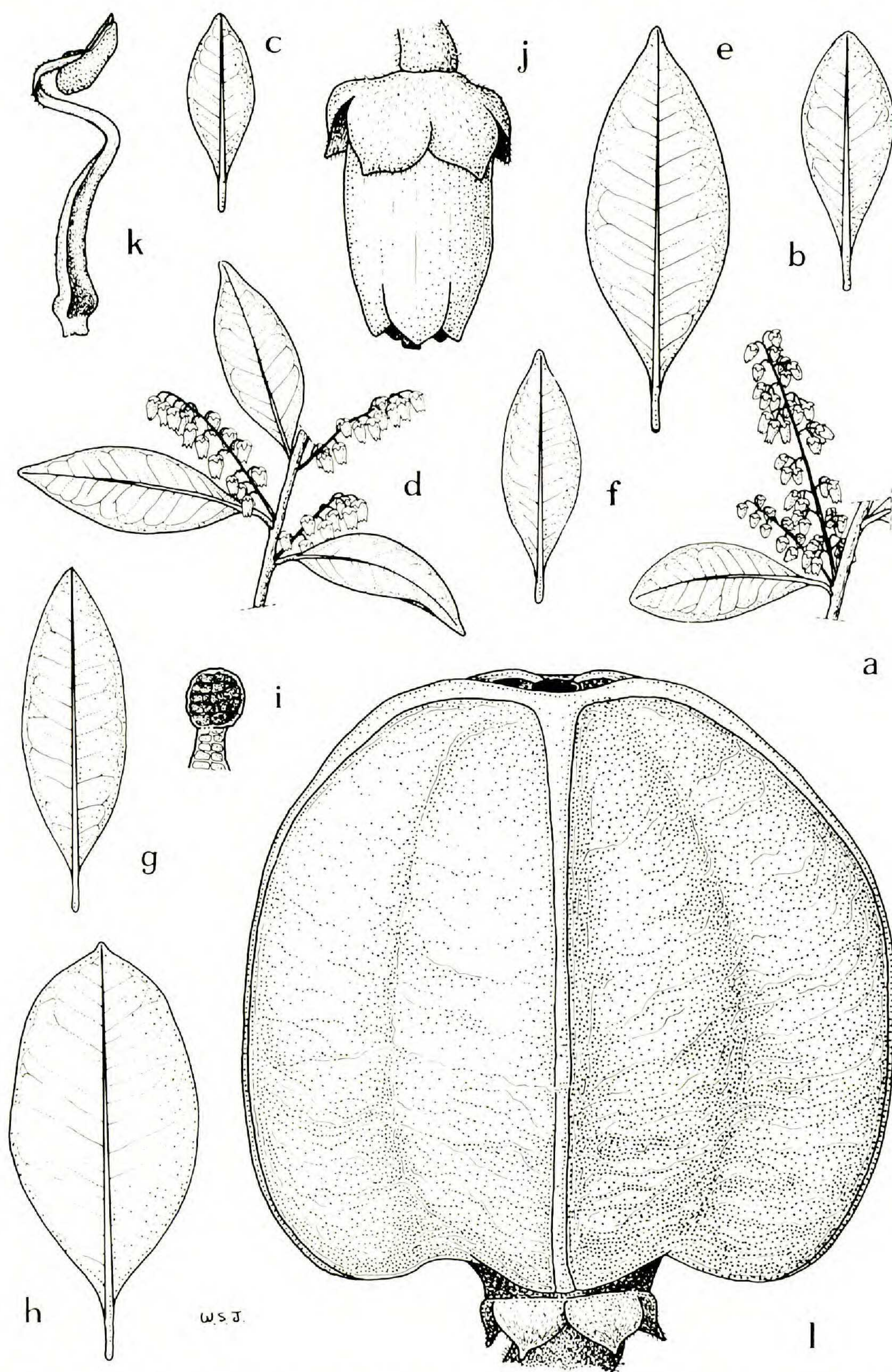


FIGURE 5. *Craibiodendron scleranthum*. a–c, var. *scleranthum*: a, segment of twig with inflorescences, $\times 0.3$; b, c, leaves, $\times 0.5$. d–l, var. *kwangtungense*: d, segment of twig with inflorescences, $\times 0.3$; e–h, leaves, $\times 0.5$; i, gland-headed hair, $\times 125$; j, flower, $\times 5$; k, stamen, $\times 10$; l, capsule, $\times 5$.

Tree or shrub to 20 m tall. Leaf blades ovate to elliptic or occasionally slightly obovate, (3.6–)4–9.6 by 1.7–4.6 cm. Inflorescences racemelike to occasionally narrow (and poorly branched) paniclelike cymes, secondary branches represented by single bracteolate flowers or 2- or 3-flowered dichasia. Abaxial surface of calyx sparsely to densely pubescent. Capsules 13–18 by 14–25 mm.

This variety was illustrated in Hu (1954).

DISTRIBUTION AND ECOLOGY. China (Guangdong and Guangxi) (MAP 1). Open shrubby areas and mixed forests, montane areas. Flowering May through June (July).

REPRESENTATIVE SPECIMENS. **China.** GUANGDONG: Ting-wu-shan, *Chun* 6363 (A), *Ho* 60080 (W), *Ting & Shih* 635 (L), *Ying* 1533 (A, UC), 1547 (A, NY, UC). GUANGXI: Seh-feng-dar Shan, S of Nan-ning, *Ching* 8293 (A, E, NY, UC, US; paratype of *C. kwangtungense* S. Y. Hu).

Craibiodendron scleranthum is most closely related to *C. yunnanense* but is easily distinguished by its blunter leaf apices, fewer-flowered racemes (i.e., lateral branches only 1- to 3-flowered), less strongly papillose corollas, and larger capsules and seeds. The two species are geographically isolated (see MAP 1).

Populations of *Craibiodendron scleranthum* are separable into two morphologically distinctive and geographically separated varieties. Variety *kwangtungense* (of China) is best distinguished from var. *scleranthum* (of Vietnam) by its abaxially pubescent calyx. In the former variety the leaves are frequently slightly larger, and they are more apt to be ovate; the inflorescences are more often(?) unbranched and racemelike. Since these are the only differences between the two taxa, they are here considered to be conspecific. The correct name for the species is thus *C. scleranthum*.

3. ***Craibiodendron henryi*** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **5**: 158. 1912. TYPE: China, Yunnan, Szemao, 6000 ft, 6 Aug., *A. Henry* 13137 (lectotype, here selected, E!; photo of lectotype, B!; isoelectotypes, A!, K! (photo at NY!), NY!, US!). FIGURE 6.

Craibiodendron mannii W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **5**: 159. 1912. TYPE: India, Assam [Meghalaya], Juudmaka Pahar, Jowai, near Jaintia Hills, 6000 ft, Aug. 1891, *G. Mann* s.n. (holotype, CAL, not seen; possible isotype, *King's Coll.* [Mann] s.n., 1891, K!).

Tree or shrub to 15 m tall. Twigs glabrous to sparsely pubescent. Buds 1–3 per node (superposed if 2 or 3), with 2 (to 4) scales. Leaves with petiole 5–15 mm long; blade elliptic to oblong or ovate (to slightly obovate), 6.3–15 by 1.5–4.6 cm, the apex long-acuminate or acuminate (to acute), the base cuneate to rounded and often slightly attenuate, the margin plane to slightly revolute, especially near base, the secondary and tertiary veins slightly raised to impressed adaxially, the midvein nearly glabrous to sparsely pubescent (throughout to only near petiole). Inflorescences paniclelike cymes 6–30 cm long, with 2 or 3 orders of branches, longest secondary branches with usually (5 or) 6 to

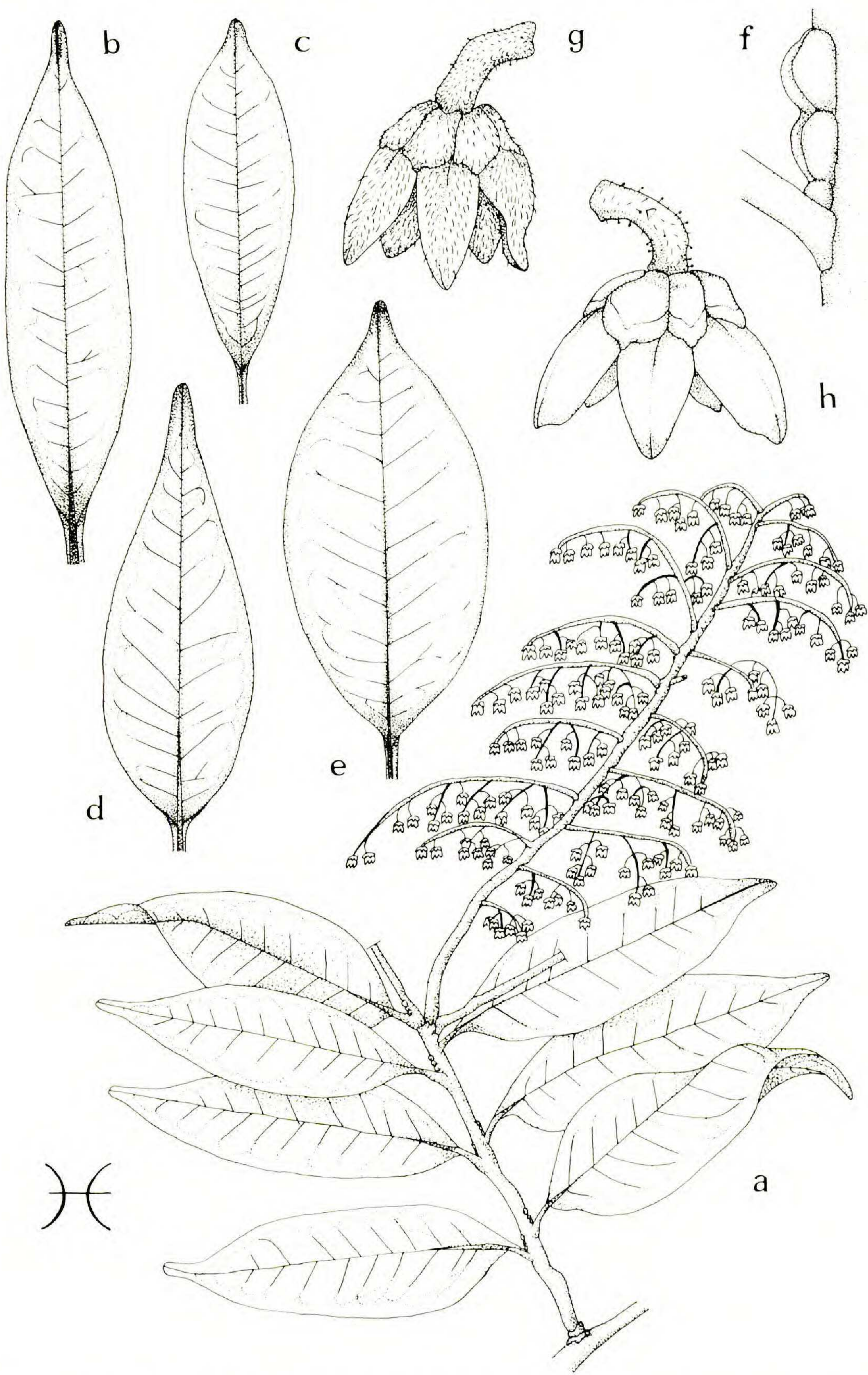
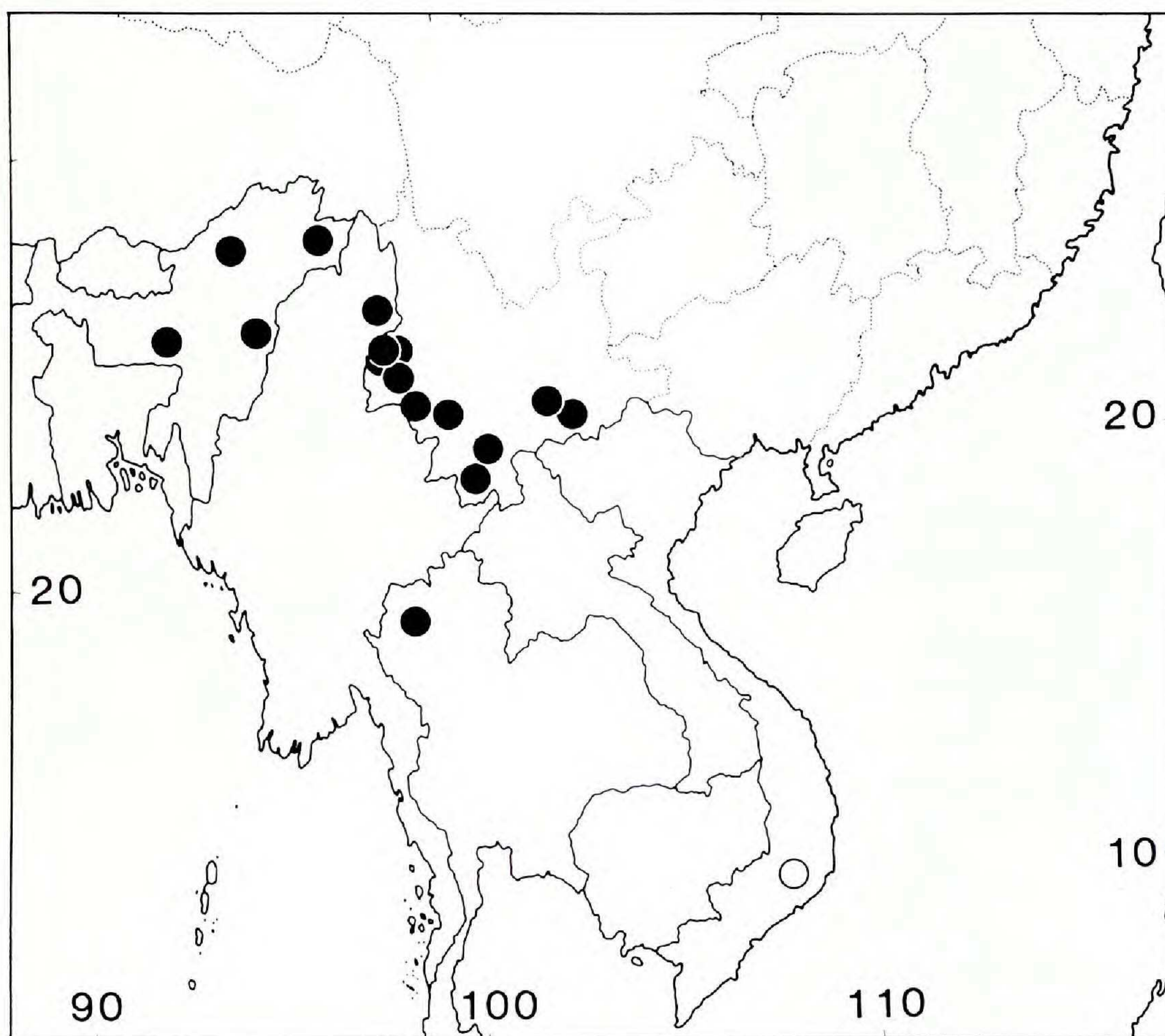


FIGURE 6. *Craibiodendron henryi*: a, segment of twig with inflorescence, $\times 0.3$; b–e, leaves, $\times 0.5$; f, superposed buds, $\times 5$; g, h, flowers, $\times 5$.



MAP 2. Distribution of *Craibiodendron henryi* (black circles) and *C. vietnamense* (open circle).

30 flowers, axes glabrous to densely pubescent. Pedicels 1–7 mm long, glabrous to densely pubescent; bracteoles alternate to subopposite, near base to midpoint of pedicel, narrowly triangular, 0.7–1.2 mm long; bracts ovate to narrowly triangular, 1.2–2.7 mm long, quickly deciduous, especially those of primary axis. Calyx lobes broadly ovate-triangular with acuminate, nearly acute, or rounded-mucronate apices, 0.8–1.5 by 1.2–2.3 mm, abaxial surface glabrous to densely pubescent; corolla campanulate, 2–3.5 by 2.1–5 mm, lobes much longer than tube, white to cream (or reddish tinged?), with abaxial surface glabrous to moderately pubescent, often obscurely papillose at margin of lobes, middle portion of each lobe sometimes with slightly thickened ridge; stamens with filament 1.5–2 mm long, anther 0.7–0.9 mm long; ovary glabrous to moderately pubescent, style glabrous. Capsules subglobose to short-ovoid, 6.5–12.5 by 9–16 mm, glabrous to sparsely pubescent; seeds 4–8.5 mm long.

DISTRIBUTION AND ECOLOGY. India (Arunachal Pradesh, Meghalaya, Nagaland), northern Burma, and northern Thailand (MAP 2). Open areas, thickets, and warm-temperate to subtropical forests; 1500–2850 m alt. Flowering (June) July through August.

REPRESENTATIVE SPECIMENS. **Burma:** Upper Burma, *Forrest* 26257 (A, E, K); Htawpaw, *Sukoe* 10096 (K). **China.** YUNNAN: NW of Tengyueh, 25°10'N, *Forrest* 8752 (A, BM, E, K); E flank of Shweli-Salwin divide, 23°20'N, *Forrest* 9434 (A, E, K); Ma-chang-kai Valley, N of Tengyueh, 25°20'N, *Forrest* 9529 (A, E, K, S); Shweli-Salwin divide, 24°50'N, *Forrest* 18391 (A, E, K, W); NW of Tengyueh, 25°20'N, 98°30'E, *Forrest* 26136 (BM, E, K); Szemao, *Henry* 9505^B (A, E, K, MO, NY); Mengtse, *Henry* 10459 (A, K, paratypes of *C. henryi*); Kien-shuei Hsien, *Tsai* 53196 (A); Chen-kang Hsien, *Wang* 72360 (A); Fo-hai, *Wang* 77404 (A); Chen-kang Snow Range, *Yü* 17070 (A, E); Mienning, Po-shang, *Yü* 18028 (A, E). **India.** ARUNACHAL PRADESH: W corner of Apa Tani Valley, Subansiri division, *Cox & Hutchinson* 521 (K); Delei Valley, *Kingdon-Ward* 7974 (K). MEGHALAYA: near Jowai, Jaintia Hills, *King's Coll. [Mann]* s.n., 1891 (K). NAGALAND: Kekrima, Naga Hills, *Bor* 2828 (K); Pedi, Naga Hills, *Bor* 6271 (K). **Thailand:** Doi Angka, *Garrett* 477 (A, BM, E, K, L).

Craibiodendron henryi shows greater infraspecific variability in unicellular indumentum than any other species in the genus. In some individuals the corollas are glabrous, while in others they are more or less moderately covered with unicellular hairs. The calyx and inflorescence axes also vary from glabrous to quite pubescent. Since these pubescence forms occur sporadically throughout the taxon's geographic range and are not correlated with any other morphological features, they have not been given formal taxonomic recognition. *Craibiodendron mannii*, a species described from northeastern India (see Rao & Chakraborti, 1982), is clearly conspecific, showing the distinctive combination of acuminate leaves and campanulate, deeply lobed corollas characteristic of *C. henryi*.

This species is most closely related to (and confused with) *Craibiodendron vietnamense* and *C. stellatum*; all three species have campanulate corollas with conspicuous lobes (see key). *Craibiodendron henryi* and *C. vietnamense* are allopatric, while *C. henryi* and *C. stellatum* are only marginally sympatric (see MAPS 2, 3). A few specimens from Sze-mao in Yunnan (*Henry* 9505^B) show some characters of *C. stellatum* (e.g., occasional leaves with apices acute to rounded and some flowers with the lobes only slightly longer than or more or less equal to the tube). Both *C. stellatum* and *C. henryi* occur in the region of southern Yunnan, and these specimens may represent hybrids. The intermediacy of these specimens was also noted by Smith (1912).

For earlier illustrations of *Craibiodendron henryi*, see Anonymous (1974) and Rao and Chakraborti (1982, under *C. mannii*).

4. *Craibiodendron vietnamense* W. Judd, sp. nov.

FIGURE 7.

Arbor ad 20 m alta. Ramuli hornotini sparsim pubescentes. Folia elliptica, oblonga vel leviter ovata, 3.4–10.2 cm longa, 1.5–4 cm lata, ad apicem acuminate, ad basin cuneata vel rotundata, ad marginem planiuscula vel leviter revoluta; petioli 7–13 mm longi. Inflorescentiae axillares, paniculatae, 7–10 cm longae, floribus terminalibus; rami secundari 7–18 floribus. Flores 5-merus. Calyx lobis 0.5–1 mm longis, 1–1.2 mm latis, abaxialiter sparsim vel moderate pubescentibus. Corolla alba, campanulata, 2.5–3.5 mm longa, 1.8–4 mm lata, lobis plus minusve aequantibus tubum, abaxialiter sparsim pubescentis, plerumque leviter papillosis. Filamenta 1.6–2 mm longa. Stylus sparsim pubescens. Capsula non visa.

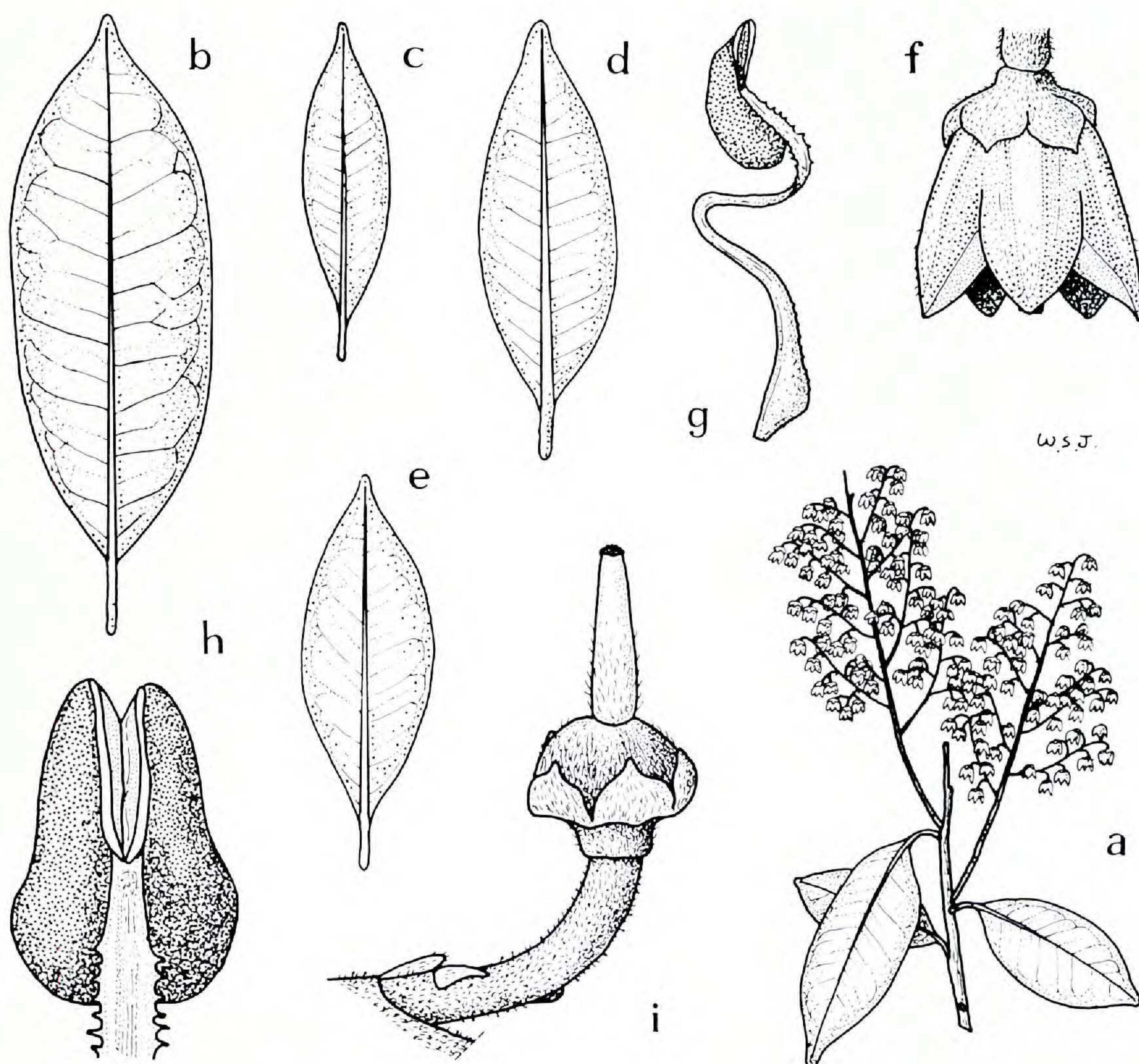


FIGURE 7. *Craibiodendron vietnamense*: a, segment of twig with inflorescences, $\times 0.3$; b–e, leaves, $\times 0.5$; f, flower, $\times 5$; g, stamen, $\times 10$; h, anther, $\times 25$; i, pedicel and gynoecium, $\times 10$.

Tree to 20 m tall. Twigs very sparsely to sparsely pubescent. Buds usually single, with 2 to 4 scales. Leaves with petiole 6–14 mm long; blade elliptic to oblong or slightly ovate, 3.4–10.2 by 1.5–4 cm, the apex acuminate, the base cuneate (to rounded), the margin plane to slightly revolute, especially near base, the secondary and tertiary veins slightly raised to impressed adaxially, the midvein very sparsely pubescent near petiole. Inflorescences paniclelike cymes 7–10 cm long, with 2 or 3 orders of branches, longest secondary branches with 7 to 18 flowers, axes sparsely to densely pubescent. Pedicels 1.5–4 mm long, moderately to densely pubescent; bracteoles alternate, from near base to midpoint of pedicel, broadly to narrowly triangular, 0.3–0.9 mm long; bracts triangular or narrowly so, 0.4–1.5 mm long, quickly deciduous. Calyx lobes broadly ovate-triangular with acuminate apices, 0.5–1 by 1–1.3 mm (possibly larger in fruit), abaxial surface sparsely to moderately pubescent; corolla campanulate, 2.5–3.5 by 1.8–4 mm, lobes more or less equal to tube, white, with abaxial surface very sparsely to sparsely pubescent, margin of lobes clearly papillose

to nearly smooth, middle portion of each lobe with thickened ridge; stamens with filament 1.6–2 mm long, anther 0.6–0.9 mm long; ovary moderately to densely pubescent, style sparsely pubescent. Capsules not seen.

TYPE: Annam [Vietnam], Massif du Bi-Doup, prov. Haut Donai, 2000 m, 15 Aug. 1940, *M. Poilane* 30927 (holotype, L!; isotype, P).

DISTRIBUTION AND ECOLOGY. Vietnam, Bi-Doup region, 2000 m alt. (MAP 2). Probably flowering July and August.

REPRESENTATIVE SPECIMENS. **Vietnam:** Massif du Bi-Doup, *Poilane* 30723 (L), 30731 (A, K, L).

Craibiodendron vietnamense is most closely related to *C. henryi* and *C. stellatum*. It is distinguished from the former by its less deeply lobed corollas and its style with a few unicellular hairs, and from the latter by its acuminate leaf apices, its slightly smaller flowers, and its pubescent style. The distinctiveness of this taxon was first recognized by Gagnepain, who considered it to be an undescribed species (unpubl. data, Herb. Leiden). The species is geographically isolated from *C. henryi* (see MAP 2); however, a southern, disjunct population of *C. stellatum* also occurs in the Bi-Doup region of Vietnam (see MAP 3).

5. ***Craibiodendron stellatum*** (Pierre) W. W. Smith, Kew Bull. **1914**: 129. 1914. FIGURE 8.

Schima stellata Pierre, Fl. Forest. Cochinchine **1**: t. 122. 1887. TYPE: Cambodia, prov. Samrong-tong, la montagne Schral, 900 m, *Pierre* 853 (holotype, P; isotype, K!).

Craibiodendron shanicum W. W. Smith, Rec. Bot. Surv. India **4**: 277. 1911. TYPE: Burma, Maymyo, 3500 ft, 3 Aug. 1908, *J. H. Lace* 4160 (lectotype, here selected, CAL, photo published in Smith (1912); photo of lectotype, B!; isoelectotypes, E!, K!).

Tree or shrub to 12 m tall. Twigs glabrous to moderately pubescent. Buds 1 or 2 per node (superposed if 2), with 2 (to 4) scales. Leaves with petiole 3–16 mm long; blade elliptic or oblong to ovate or obovate, (3–)4–17 by (1–)1.7–8 cm, the apex retuse to rounded or acute, the base cuneate to rounded (or slightly attenuate), the margin plane to revolute, the secondary and tertiary veins slightly raised to clearly impressed adaxially, the midvein sparsely pubescent, at least proximally. Inflorescences paniclelike cymes, 5–22 cm long, with 2 or 3 orders of branches, longest secondary branches with (7 or) 8 to 25 flowers, axes moderately to densely pubescent. Pedicels 1.5–6 mm long, moderately to densely pubescent; bracteoles alternate to opposite, near base to midpoint (to near apex) of pedicel, narrowly triangular, 0.4–1 mm long; bracts ovate to narrowly elliptic, narrowly triangular, or linear, 0.8–6.5 mm long, quickly deciduous (especially those of primary axis). Calyx lobes broadly ovate-triangular with acuminate to rounded-mucronate apices, 0.8–2.5 by 1.1–2.5 mm, abaxial surface moderately to densely pubescent; corolla campanulate, 3–4.5 by 2.5–5.5 mm, lobes more or less equal to tube, white or cream, with abaxial surface moderately to densely pubescent, often obscurely papillose at margin of lobes, middle portion of each lobe usually with slightly thickened

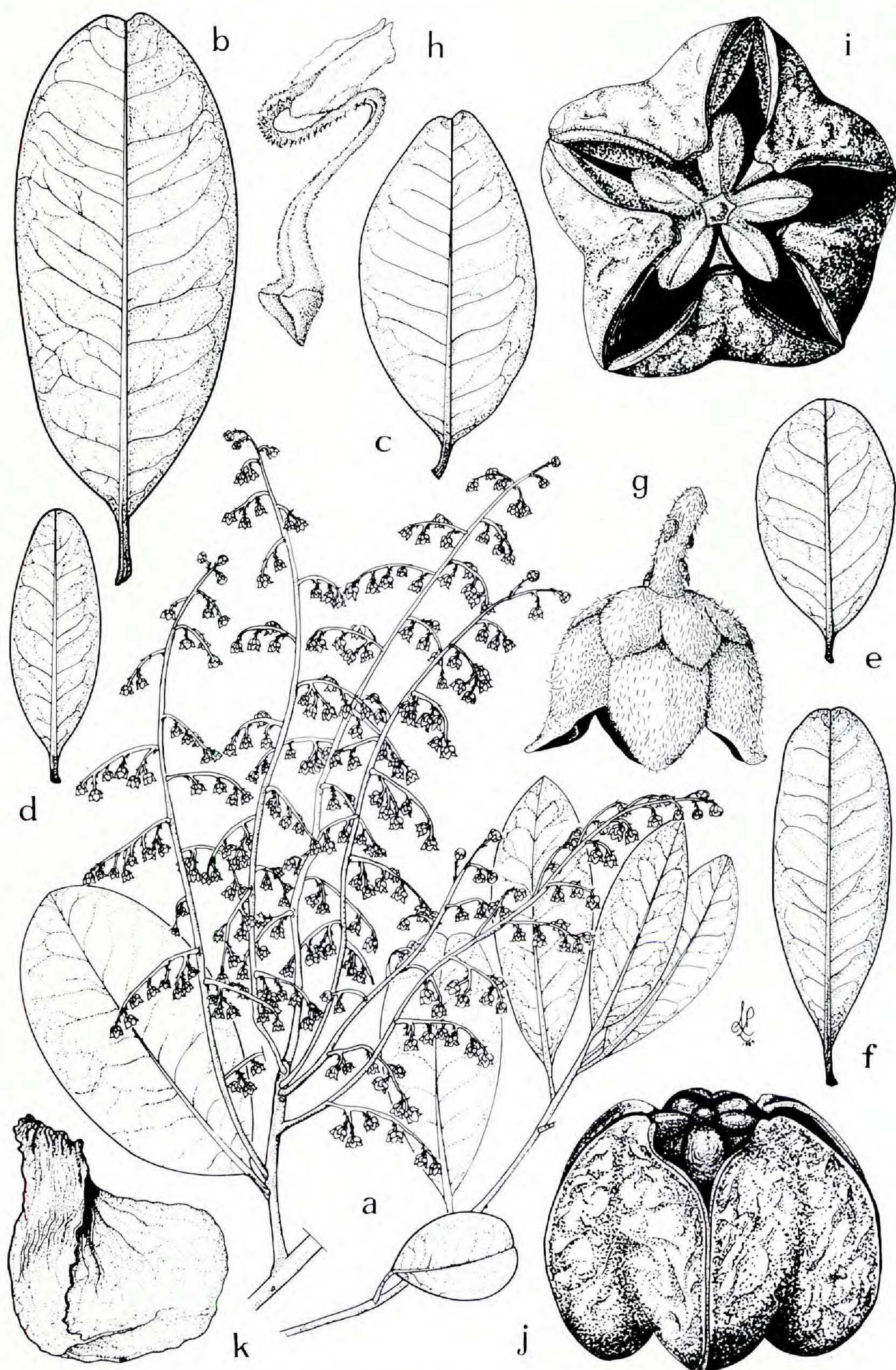
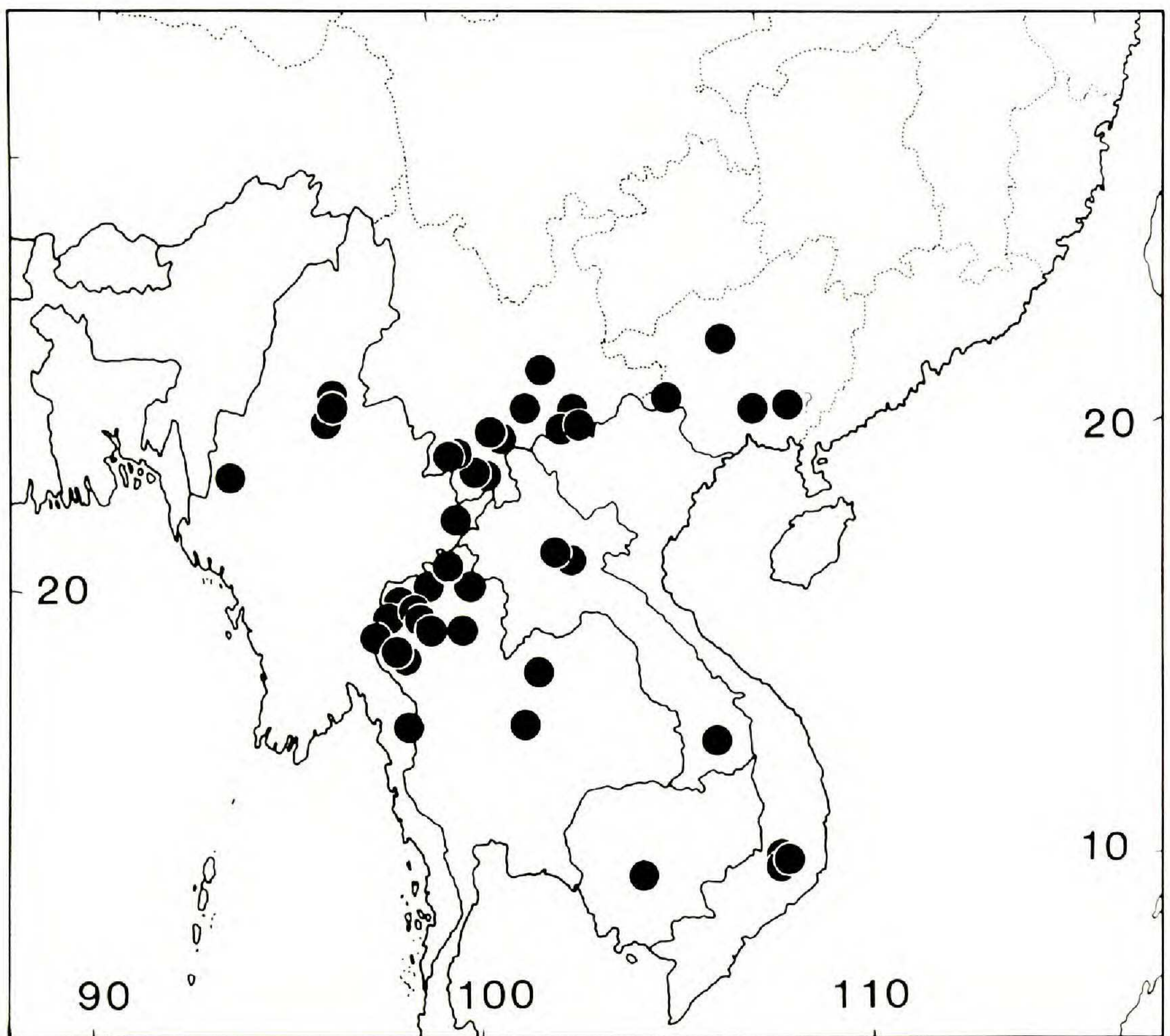


FIGURE 8. *Craibiodendron stellatum*: a, segment of twig with inflorescences, $\times 0.3$; b–f, leaves, $\times 0.5$; g, flower, $\times 5$; h, stamen, $\times 10$; i, j, capsule, top and side views, $\times 5$; k, seed with unilateral wing, $\times 10$.



MAP 3. Distribution of *Craibiodendron stellatum*.

ridge; stamens with filament 1.8–2.7 mm long, anther 0.7–0.9 mm long; ovary densely pubescent, style glabrous. Capsules subglobose to short-ovoid, 6–13 by 10–20 mm, very sparsely to sparsely pubescent; seeds 5–10 mm long.

DISTRIBUTION AND ECOLOGY. China (Guangxi, Yunnan), Burma, Laos, Thailand, Cambodia, and Vietnam (MAP 3). Thickets and open areas, savannas, dry dipterocarp forests, warm-temperate to subtropical forests; 200–1950 m alt. Flowering chiefly (June) July through October.

Vidal (1960) recorded that in Laos *Craibiodendron stellatum* forms a co-dominant in savannas with *Lyonia ovalifolia* (Wallich) Drude and *Castanopsis ferox* Spach and is a characteristic small tree—along with *Lyonia ovalifolia*, *Vaccinium exaristatum* Kurz, *Helicia balansae* Lecomte, and *Anneslea fragrans* Wallich—in forests of *Quercus* spp. and *Keteleeria rouletii* (A. Chev.) Flous. Wang (1939) reported the species as an understory shrub with species of *Lyonia*, *Wendlandia*, *Woodfordia*, *Eurya*, *Ternstroemia*, *Cudrania*, *Phyllanthus*, and *Callicarpa* in forests of *Quercus*, *Castanopsis*, *Pasania*, and *Schima*. It is also common in forests dominated by species of *Dipterocarpus*.

REPRESENTATIVE SPECIMENS. **Burma:** Falam, *Gale* 9195 (E); Maymyo Hill, *Khan* 117 (K); Mindat, *Kingdon-Ward* 22489 (BM); Maymyo Plateau, *Lace* 3128 (A, E, K); Amherst distr., Dawna Range, *Lace* 5669 (E, K); Loimwe, S Shan states, *MacGregor* 726 (E, paratype of *C. shanicum* W. W. Smith). **China.** GUANGXI: Chin Tung, W of Hoo-chih, *Ching* 6461 (E, NY); Kwei Hoo Poo, S of Hin-yen, *Ching* 7294 (E, NY); Pin-lam, *Ko* 55539 (A); Chen-pien distr., *Ko* 55955 (A). YUNNAN: Man-hao, *Handel-Mazzetti* 5875 (w); Mengtze, *Henry* 9505 (A, E, K, MO, US); E of Szemao, *Rock* 2799 (A); T'sing-pien, *Tsai* 52597 (A); Ping-pien Hsien, *Tsai* 60560 (A, E); Che-li Hsien, *Wang* 75854 (A); Lantsang Hsien, *Wang* 76641 (A); Fo-hai, *Wang* 77323 (A); Tung-hai, *Wissmann* 45 (w). **Laos:** Muong-you, Luang-prabang, *Spire* s.n. (P?, reported by Vidal, 1960). **Thailand:** prov. Chiang Mai, S side of Doi Suthep, 18°50'N, 98°54'E, *Abbe et al.* 9307 (A, E, L); distr. Chaiphum, Tunkamong, 16°20'N, 101°45'E, *Van Beusekom et al.* 4361 (K, L, MO); distr. Phrae, Mae-hray, 17°45'N, 100°15'E, *Van Beusekom et al.* 4819 (K, L, MO); Ban Kae, 7 km S of Mae Chem, *Hansen et al.* 11052 (L); Doi Chong, 19°25'N, 98°18'E, *Hansen & Smitinand* 12630 (K, L); Chiang Mai, Doi Sootep, *Kerr* 1282 (BM, K, L; paratypes of *C. shanicum*), 1282A (BM, E, K; paratypes of *C. shanicum*); Kao Krading, *Kerr* 20060 (BM, E, K); S of Bo Luang, Om Koi trail, 18°04'N, 98°22'E, *Larsen et al.* 1952 (L); between Hang Dong and Bo Luang, 18°17'N, 98°30'E, *Larsen et al.* 2147 (L); NW of Chieng-mai, 19°N, 98°30'E, *Nooteboom* 692 (K, L); Doi Chiengdao, *Put* 4532 (BM, E, K, L); Pang Kia, *Rock* 1604 (A, UC); Doi Sutep, Chieng-mai, *Sørensen* 4805 (A, L); between Ban Khun Tan and Doi Khun Tan, *Tagawa et al.* 9096 (L). **Vietnam:** Massif du Langbian, de Xomgoma à Dran, *Chevalier* 38542 (L); Dalat, *Evrard* 246 (A); Massif du Bi-Doup, prov. Haut-Donai, *Poillane* 30248 (L); N of Dalat, prov. Haut-Donai, *Poillane* 30401 (K, US).

Craibiodendron stellatum is most closely related to *C. henryi* and *C. vietnamense* and is distinguished from both by its leaves with rounded to retuse or acute (vs. usually acuminate) apices and its larger corollas. In addition, it differs from *C. henryi* in its more shallowly lobed corollas, and from *C. vietnamense* in its glabrous style. The most widely distributed species in the genus (see MAP 3), it is most common from southern Yunnan south to northern Thailand. The species is slightly sympatric (and may occasionally hybridize) with *C. henryi* at the northern edge of its range (in southern Yunnan) and occurs with *C. vietnamense* in the Bi-Doup region of Vietnam.

Craibiodendron stellatum has been more frequently collected than any of its congeners and was first to be described (see Pierre, 1887; Smith, 1911).

This species has previously been illustrated in Pierre (1887), Smith (1912), Dop (1930), and Anonymous (1974).

SPECIES EXCLUDED FROM CRAIBIODENDRON

Craibiodendron forrestii W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 5: 160. 1912. = *Quercus* sp.

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